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Blocking between landmarks during 2-D (touchscreen) and 3-D (ARENA) search tasks with pigeons

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Abstract Many studies investigating cue competition have focused on the blocking effect. We investigated the blocking effect with pigeons using a landmark-based spatial search task in both a touchscreen preparation (Exp. 1a) and an automated remote environmental navigation apparatus (Exp. 1b). In Phase 1, two landmarks (LMs: A and Z) appeared on separate trials as colored circles among a row of eight (touchscreen) or six (ARENA) identical response units. Subjects were rewarded for pecking at a target response unit to the right of LM A and to the left of an extraneous LM, Z. During the blocking trials in Phase 2, LM X was presented in compound with a second LM (A) that had been previously trained. On control trials, LM Y was presented in compound with LM B and a target in the same manner as in the trials of AX, except that neither landmark had previously been trained with the target. All subjects were then tested with separate trials of A, X, B, and Y. Testing revealed poor spatial control by X relative to A and Y. We report the first evidence for a spatial-blocking effect in pigeons and additional support for associative effects (e.g., blocking) occurring under similar conditions (e.g., training sessions, spatial relationships, etc.) in 3-D and 2-D search tasks.

Keywords Blocking · Spatial learning · Cue competition · Navigation · Generalization

Most vertebrate species navigate their environment for a variety of reasons, such as to search for food, find mates, and

avoid predators. Such movement often necessitates that the animal keep track of where it has been, where it is going, and how to return home. One method of doing this is to learn to use spatial cues, such as beacons and landmarks (Leising & Blaisdell, 2009). Spatial learning has been demonstrated in virtually all vertebrates studied, but the learning process itself has been less well characterized. Although some have argued for specialized spatial-learning systems or modules (Cheng, 1986; O’Keefe & Nadel, 1978), others have suggested that more general-purpose associative-learning processes may govern spatial learning (e.g., Leising & Blaisdell, 2009; Miller & Shettleworth, 2007). The latter proposal has been supported through the search for commonalities between spatial learning and more conventional associative-learning paradigms, such as Pavlovian and instrumental conditioning.

The blocking effect is a hallmark of associative-learning processes (Kamin, 1969; Moore & Schmajuk, 2008). In blocking, cue A, such as a conditioned stimulus (CS), is trained as a predictor of an outcome, such as an unconditioned stimulus (US). After CS A has acquired a conditioned response through pairings with the US, additional A–US pairings are given in the presence of another CS (X). That is, the subject first receives A–US pairings, followed by AX–US pairings. When the subject is subsequently tested on X alone, much less conditioned responding is observed than in a control group. One type of control group, used in a between-subjects demonstration of blocking, is to omit the Phase 1 A–US pairings and only give AX–US pairings. Responding to X at test is greater in the control than in the blocking group, for which A had been pretrained prior to AX–US pairings. A second control consists of a within-subjects design, with the subject receiving A–US pairings in Phase 1 of training, and then AX–US pairings alternated with BY–US pairings in Phase 2 of training. Then subjects are tested separately on X and Y. Greater conditioned responding to Y than to X indicates that conditioning to X was blocked by pretraining of A,

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whereas Y was not blocked by B, which had no pretraining. In a spatial task, a landmark acts as a CS that reliably predicts an upcoming US, but additionally, it provides stable information regarding the location of the US (e.g., Ruprecht, Wolf, Quintana, & Leising, 2014). Conventional blocking is evaluated in terms of the magnitude of responding elicited by the blocked cue; however, spatial blocking is evaluated in terms of spatial accuracy. Blocking of spatial control by a landmark has been demonstrated in rats using arrays of landmarks in an open field (Biegler & Morris, 1999; Stahlman & Blaisdell, 2009), as well as using extra-maze cues in a Morris pool (Rodrigo, Chamizo, McLaren, & Mackintosh, 1997) and radial-arm maze (Chamizo, Sterio, & Mackintosh, 1985). No studies demonstrating spatial blocking have been reported with an avian species.

There is reason to believe that pigeons are likely to show evidence of spatial blocking. Pigeons' spatial abilities have been extensively studied, and laboratory tasks have shown that pigeons readily learn to use a landmark (LM) to find a hidden target (e.g., a food goal; e.g., Cheng & Spetch, 1995). Evidence has also been found in pigeons for spatial overshadowing, in which spatial control by a landmark was reduced by the presence of a more proximal landmark (Leising, Garlick, & Blaisdell, 2011; Spetch, 1995, Spetch & Mondloch, 1993). We recently reported two spatial-overshadowing experiments using operant training in either a touchscreen chamber (Leising et al., 2011, Exps. 1 and 2) or an automated open-field ARENA (Leising et al., 2011, Exp. 2). These results suggest that associative processes govern spatial learning, and that these processes operate similarly in three-dimensional (3-D; ARENA) and two-dimensional (2-D; touchscreen) tasks. The present studies investigating the blocking effect borrowed heavily from those previously used in our laboratory to demonstrate spatial overshadowing (Leising et al., 2011).

In Experiments 1a and 1b, we used a within-subjects design, in which subjects learned in Phase 1 of training to locate hidden targets by using landmarks as discriminative spatial cues. Previous studies investigating blocking in appetitive conditioning have shown a considerable degree of generalization between stimuli (e.g., Ganesan & Pearce, 1988). In the present experiments, we trained pigeons to respond at a target to the left of one landmark and to the right of another in Phase 1. This type of discrimination training should attenuate the presence of any side bias, as well as attenuate generalization across landmarks by requiring subjects to learn about the qualities of each landmark. In Phase 2, all birds searched for the target in the presence of a compound of LM A and a novel LM X on some trials (AX), and on other trials in the presence of a compound of two novel LMs (BY). Following Phase 2 acquisition, pigeons received nonreinforced probe tests of each landmark separately. If pretraining of A were to block spatial control by X, then at test we would expect to see poorer spatial control by X than by A and, more critically, by Y.

Experiments 1a and 1b

In Experiments 1a and 1b, we also investigated whether a blocking effect observed with a 2-D touchscreen task (Exp. 1a) would be observed using identical experimental parameters within a “real-space” 3-D task (Exp. 1b). Though differences have been found in the patterns of spatial control by landmarks in a touchscreen-equipped chamber and an open field (e.g., Lechelt & Spetch, 1997), most studies have revealed more similarities than differences (e.g., Spetch, Cheng, & MacDonald, 1996; Leising et al., 2011). We recently reported analogous findings on the overshadowing effect with pigeons in a touchscreen-equipped chamber and an automated remote environmental navigation apparatus (ARENA—i.e., an automated open field: Leising et al., 2011; see Leising, Garlick, Parenteau, & Blaisdell, 2009, for more details on ARENA). ARENA allows subjects to travel through open space to interact with landmarks and response units, and thus provides a more ecologically valid 3-D search task with which to compare performance to the more commonly used touchscreen-equipped apparatus.

Pigeons in each apparatus received the same blocking procedure, but the methods of response detection, stimulus delivery, and reward retrieval differed between the apparatus. In Experiment 1a, pigeons pecked at a row of eight circular visual response units on a touchscreen-equipped display (see Fig. 1). The response unit locations were defined by a white border against a black background. Landmarks within the units were displayed as colored response units. In Experiment 1b, pigeons pecked at a row of six plastic ARENA response modules on the floor of an open-field testing area (see Fig. 1). The response unit locations were defined by a recessed well in the center of each module. Landmark modules were defined within the row of response units by colored lights generated by LEDs located within the recessed well of each module.

Method

Subjects

Five white Carneaux pigeons (*Columba livia*; Double T Farm, IA) served as subjects in the touchscreen apparatus (Exp. 1a). They were naive to the present procedure, array, and colored landmarks, but had previously participated in a touchscreen task. Four white Carneaux pigeons (*Columba livia*; Double T Farm, IA) served as subjects in ARENA (Exp. 1b). These subjects had previously served in conditional discrimination (Leising et al., 2009) and overshadowing (Leising et al., 2011) procedures in ARENA. The pigeons in Experiments 1a and 1b were maintained at 85 % of their free-feeding weights. They were individually housed in a colony with a 12-h light:dark

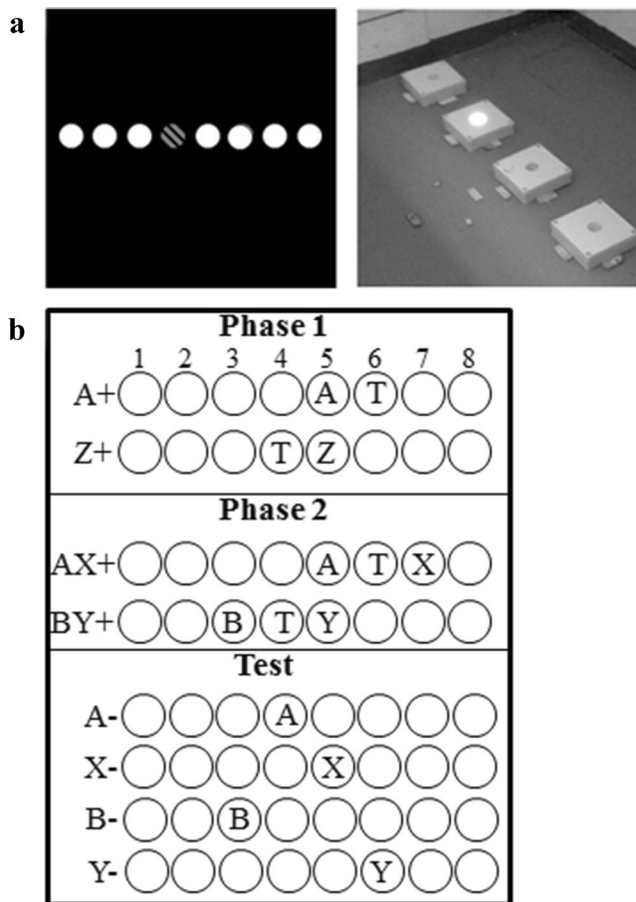


Fig. 1 **a** The left-hand panel is an example of the display used for the touchscreen spatial task in Experiment 1a. The eight response units are shown, including one landmark at Position 4. The right-hand panel is a photo of four (of the six) ARENA modules in the test area (reprinted with permission from Leising et al., 2011) in Experiment 1b. **b** Schematic of the experimental design. The letters A, X, Y, and B denote different colored landmarks, and T indicates the location of the target. The use of “+” indicates the opportunity for reinforcement, whereas the use of “-” indicates no opportunity for reinforcement. Numbers along the top denote unit positions along the linear array of eight units (Exp. 1a) or six modules (Exp. 1b). The figures are not drawn to scale

cycle and were provided with free access to water and grit. Experimental procedures occurred during the light portion of the cycle.

Apparatus

Experiment 1a was conducted in a flat-black Plexiglas chamber (38.0 cm wide \times 36.0 cm deep \times 38.0 cm high). All stimuli were presented by computer on the LCD monitor (NEC MultiSync LCD1550M) visible through a 23.2 \times 30.5 cm viewing window in the middle of the front panel of the chamber. The bottom edge of the viewing window was 13.0 cm above the chamber floor. Pecks to the monitor were detected by an infrared touchscreen (Carroll Touch, Elotouch Systems, Fremont, CA) mounted on the front panel. A 28-V

houselight located in the ceiling of the box was illuminated at all times. A food hopper (Coulbourn Instruments, Allentown, PA) was located in the center of the front panel, its access hole flush with the floor. All experimental events were controlled and recorded with a Pentium-III-class computer (Dell, Austin, TX). A video card controlled the monitor in the SVGA graphics mode (800 \times 600 pixels).

A row of eight units 2.0 cm in diameter served as the stimuli (see Fig. 1a). All eight units were defined by a white border against a black background. The units were separated by 3.0 cm center to center, and the edges of the row were centered with respect to the monitor. A response area was defined by an invisible border that extended 2.0 mm beyond the visible border of each unit. A 2.0-mm² black square was centered within each unit. This black square was not present when a disk served as a landmark. A unit serving as a response unit was filled white to 35 % of its total possible brightness, or intensity. A unit serving as a landmark was filled with a texture and color. The colors were pure green, blue, and red, as well as orange (RGB: 255, 102, 51). The graphic textures were leaves (green), scales (blue), 3-D cubes (red), and interconnected rectangles (orange). Assignments of colors to landmarks were counterbalanced across birds.

Experiment 1b was conducted in a sound-attenuating room with a 2.3 \times 1.5 m test area. ARENA included the testing room, six ARENA modules, and a holding cage with a grain hopper. A white-noise generator provided background noise [56–63 dB (A)] in the testing area. A Sony SSC-DC374 color video camera with a wide-angle lens was mounted on the ceiling 2.4 m above the floor of the test area and allowed for the viewing and recording of experimental procedures in an adjacent room. A 31.8 \times 16.7 cm automated pet door was mounted on one wall of the testing room and led to a holding cage with a hopper identical to that described in the touchscreen task mounted on the rear wall. The walls, floor, and ceiling of the holding cage were made of white acrylic, and the holding cage was illuminated by a 28-V Med Associates houselight.

Stimulus presentation and response detection were accomplished by the modules (Badelt & Blaisdell, 2008; Leising et al., 2009; see Fig. 1a). Each module was a square plastic box measuring 12.9 cm wide and 3.5 cm high. A well measuring 3.0 cm in diameter by 3.0 cm in depth was created in the center of the module. A sensor circuit, including sensing and reference electrodes, was enclosed within the module. The sensing field was restricted to the volume within the cup (described in more detail in Badelt & Blaisdell, 2008). The sensor was activated when a pigeon’s beak (or any conductive mass) broke the top planar surface and entered the space within the well. The module also housed a transmitter and receiver, which communicated with a PC computer in an adjacent room using radio waves. The network allowed each module to receive command signals, change the status of the LEDs, and send detection events to the computer. Each

module was equipped with six LEDs located in the bottom of the response area. Three of the bulbs were positioned horizontally, and the remaining bulbs were positioned vertically facing up toward the opening of the well. The vertical bulbs were used to present colored lights to serve as visual landmarks. The response and stimulus areas of a module were defined by the perimeter of the recessed well. Six modules served as response units, positioned in a single row and spaced 31.4 cm center to center. The midpoint of the six units was centered at an imaginary line perpendicular to the food hopper in the holding cage. All units were 100.3 cm from the south wall of the test area and 49.5 cm from the north wall.

The colors used within the modules were sky blue (RGB: 102, 255, 255), lime green (RGB: 153, 255, 000), magenta (RGB: 153, 51, 255), orange (RGB: 255, 102, 51), and firebrick (RGB: 178, 34, 34). The color for Z was orange for each subject. Assignments of colors to landmarks for the remaining colors were counterbalanced across birds.

Procedure

All procedural details (Phase 1, Phase 2, and test) were the same for the touchscreen and ARENA preparations, with the exception of the use of 3-D modules as response locations and food retrieval from a separate area in ARENA. All subjects had been previously trained to retrieve mixed grain and pellets from a food hopper. At the beginning of the experiment, pigeons were trained to search for a target unit among the other response units. On each trial, one unit was randomly selected without replacement to be the target and was filled white at full brightness (RGB: 255, 255, 255). Pecks to all response units were recorded during a trial. Search training progressed in stages, during which we manipulated both the schedule of reinforcement and the brightness of the target (see Leising et al., 2011, for details). The schedule of reinforcement increased across stages, from continuous (CRF); to a modified fixed ratio 2 (FR-2), which required two consecutive pecks to the target; and finally, to an FR-2 followed by a fixed interval (FI) of 8 s. The FI period was initiated after the second consecutive peck to the target (thereby meeting the FR-2 criterion), and the trial terminated with reinforcement after one additional peck to the target following the 8-s interval. The brightness of the target was progressively dimmed across training from full brightness to 78 %, and then 61 %. During this portion of training, the target unit was always brighter than the nontarget response units, which were lit to 35 % brightness. Subjects advanced to a new reinforcement schedule and a dimmer target disk after ten consecutive correct trials, or regressed after five consecutive incorrect trials. Sessions lasted for 72 trials or 60 min. All trials were followed by a variable-time (VT) 15-s intertrial interval (ITI). One session with 80 % of trials ending in reinforcement was required in order to advance to landmark training.

Phase 1 All subjects were trained with two landmarks with stable spatial relationships to a hidden target in Phase 1. On A + trials, the target was located one unit to the right of A, whereas the target was located one unit to the left of Z. Each session consisted of 80 trials (40 trials each of A and Z). The position of the target was selected pseudorandomly from Units 2–7 in Experiment 1a and from Units 2–5 in Experiment 1b, thereby determining the location of A or Z. There was an unstable relationship between the location of the target and the other cues in the operant box (e.g., the frame of the display), but the spatial relationship between the landmark and the target remained stable across trials. Initially, the target was filled white at full brightness, and pecks were reinforced according to a FR-2 + variable-interval (VI) 4-s schedule of reinforcement. In the VI schedule, the duration of the interval was randomly selected from a range of 1–7 s (in steps of 1 s). Trials terminated with the requisite number of pecks at the target, 30 cumulative incorrect pecks to any unit, or after 60 s. All trials were followed by a VT 15-s ITI. Each session consisted of 80 trials (40 trials each of A and Z, intermixed) or terminated after 60 min, whichever came first.

As in search training, the target was progressively dimmed within and across sessions to 78 %, 61 %, and finally 35 % brightness, at which point the target was indistinguishable from the rest of the response units. With the target and nontarget locations at 35 % brightness, the schedule of reinforcement was concurrently increased from CRF, to a modified FR-2, and finally to FR-2 + VI-4. Subjects advanced to a new reinforcement schedule and a dimmer target disk after ten consecutive correct trials, or regressed after five consecutive incorrect trials. Each subject was advanced independently to Phase 2 after it had completed two consecutive sessions in which the FR-2 + VI-4 reinforcement criterion was met on 80 % of trials and the mean proportion of pecks at the target (pecks at the target location divided by all responses) was greater than or equal to .60.

Phase 2 All subjects received 40 compound trials of A paired with a novel landmark, X (AX+), intermixed with 40 compound trials of two novel landmarks, B and Y (BY+) in each session. The position of A relative to the target was identical to that in Phase 1. During AX trials, X was positioned at the same distance from the target as A, but on the opposite side of the target from A. LMs B and Y were positioned in the same manner as A and X, respectively. As in previous training, the target was progressively dimmed across training to 78 %, 61 %, and finally 35 % brightness. The schedule of reinforcement was also increased from CRF, to a modified FR-2, and finally to FR-2 + VI-4. Trials terminated with the requisite number of pecks at the target, 30 cumulative incorrect pecks to any unit, or after 60 s. All trials were followed by a VT 15-s ITI. Sessions lasted for 80 trials or 60 min, whichever came first. Each subject was advanced independently to the test

phase after the reinforcement criterion was met on 80 % of trials and the mean proportion of pecks at the target (pecks at the target location divided by all responses) was greater than or equal to .60.

Test All subjects received two test sessions with three nonreinforced test trials of LMs X, A, B, and Y alone in each test session. Each test session consisted of 44 trials, with 16 reinforced trials of AX and BY, as in Phase 2 (32 total baseline trials), intermixed with 12 test trials. On a test trial, the second peck of the trial initiated an 8-s interval, after which the trial terminated without reinforcement (cf. Leising et al., 2011; Spetch, 1995). Test trials automatically terminated after 30 s if subjects failed to meet the response requirement. The order of trials and the position of the target on each trial were counterbalanced across subjects. During testing, the target location was always selected to be at either Position 4 or 5 in Experiment 1a or at Position 3 or 4 in Experiment 1b.

Measures The difference between the proportions of pecks at the target side (predicted target) and opposite side (generalization target) of the landmark during each trial was calculated as a measure of spatial control by each landmark. We did this to differentiate between the spatial control of each cue as a landmark, on the one hand, and as a beacon, on the other (cf. Mackintosh, 2002). The proportions of pecks at the predicted and generalization targets during each test trial were calculated by dividing the number of pecks at the predicted or generalization target by the number of pecks at all of the locations. To calculate a difference score, we then subtracted the proportion of pecks at the generalization target from the proportion of pecks at the predicted target. The difference from 0 indicates the strength of spatial control (i.e., larger values indicating greater spatial control), and the sign of the value indicates the direction of control (i.e., positive values indicate more responses in the direction of the predicted goal).

Results and discussion

In the touchscreen preparation, one subject failed to complete Phase 1 after 20 additional sessions of training ($n = 4$ in Exp. 1a). In ARENA, during testing, one of the modules (Module 4) became unresponsive (e.g., no illumination or response detection) for the entire duration of a test session for one bird ($n = 3$ in Exp. 1b). All analyses are reported with the remaining subjects combined and with Apparatus included as a between-subjects factor ($N = 7$). The mean numbers of training sessions required to advance to testing in Phase 1 (ARENA: $M = 14.7$, $SD = 3.1$; touchscreen: $M = 17.5$, $SD = 7.23$) and Phase 2 (ARENA: $M = 3.7$, $SD = 2.08$; touchscreen: $M = 4.5$, $SD = 2.4$) were similar in both procedures (see Fig. 2). In Experiment 1a, the reinforcement

criterion was met on 94 % ($SD = 2.80$) of trials during Phases 1 and 2, and the mean proportion of pecks at the target increased from .32 ($SD = .04$) during the first session of Phase 1 to .70 ($SD = .16$) during the last session. The reinforcement criterion was met on 91 % ($SD = 1.18$) of trials during the test sessions. In Experiment 1b, the criterion was met on 98 % ($SD = 0.30$) of trials during training and testing, and the mean proportion of pecks at the target increased from .22 ($SD = .11$) during the first session of Phase 1 to .60 ($SD = .03$) during the last session.

Figure 3 displays the mean difference scores for each landmark at test. LM A exerted greater spatial control than X, with B and Y demonstrating levels of spatial control intermediate to those of A and X. A $2 \times 2 \times 2$ mixed model analysis of variance conducted on the difference scores, with Apparatus (touchscreen or ARENA) as a between-subjects factor and Condition (blocking and control) and Landmark (A/B or X/Y) as repeated measures factors, revealed main effects of condition, $F(1, 5) = 7.55$, $p = .04$, $\eta^2 = .60$, and landmark, $F(1, 5) = 22.51$, $p = .005$, $\eta^2 = .82$, and a Condition \times Landmark interaction, $F(1, 5) = 12.60$, $p = .02$, $\eta^2 = .72$, but did not reveal a main effect of Apparatus or the interaction of Apparatus with any other factor. Although the comparison was underpowered (i.e., small samples), the data in Fig. 3 indicated very similar patterns of responding across experiments, and a power analysis using the root-mean square error of estimation of the three-way interaction indicated that 225 subjects would be required to detect the interaction. We then

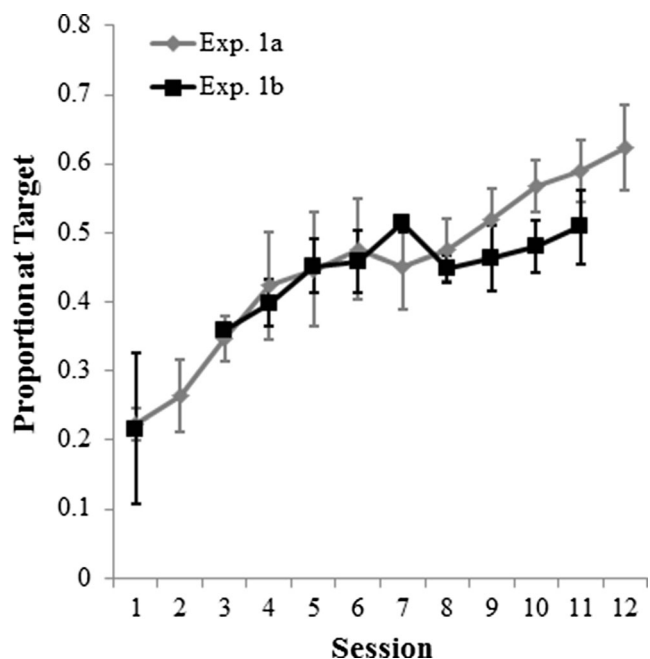


Fig. 2 Mean proportions of responding to the predicted target on trials of LMs A and Z across the sessions of Phase 1 for subjects with the touchscreen (Exp. 1a) and ARENA (Exp. 1b). Only sessions in which all subjects contributed data are displayed for each experiment. Error bars represent the standard errors of the means

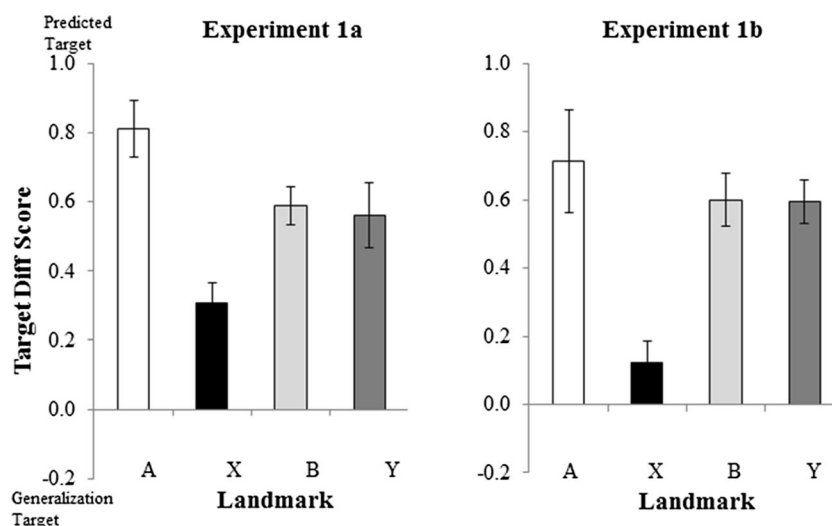


Fig. 3 Mean difference scores (proportions of responding to the predicted target minus the generalization target) during testing for each landmark in Experiment 1a (left panel) and Experiment 1b (right panel). Error bars represent the standard errors of the means. The absolute value of the

difference score indicates the strength of spatial control, whereas the sign indicates the preference to respond at the predicted or the generalization target.

collapsed across apparatus and conducted planned comparisons to isolate the source of the interaction. Spatial control was greater by A than by X, $F(1, 6) = 32.21, p = .001, \eta^2 = .84$, and by B, $F(1, 6) = 8.14, p = .03, \eta^2 = .58$. No statistical difference was apparent between spatial control by B versus Y, $F < 1.0$. Critically, spatial control was poorer by X than by Y, indicating a blocking effect, $F(1, 6) = 12.31, p = .01, \eta^2 = .67$. We compared the difference scores for each landmark to zero using single-samples t tests, which revealed that all landmarks exerted reliable spatial control over responding, $ts(5) > 4.28, ps < .01, ds > 1.51$.

A pilot experiment revealed that training on only LM A in Phase 1 resulted in a large amount of generalization to the other landmarks during test. Training with two landmarks in Phase 1 of the present experiments, such that correct responses were required to the left and right of a landmark, reduced potential generalization from A and increased the spatial control by each landmark. An evaluation of spatial control revealed a clear blocking effect. Training of spatial control by LM A in Phase 1 resulted in blocking of spatial control by X. LM Y, however, did not show diminished spatial control relative to B, which did not receive prior training. This is, to our knowledge, the first clear demonstration of spatial blocking in a touchscreen or open-field preparation with pigeons. This extends the evidence for cue competition phenomena, such as overshadowing, in spatial learning, providing further evidence for the operation of associative processes in spatial learning. Interestingly, we also observed stronger spatial control by LM A than by B. This difference was likely due to more training with A (Phase 1 and 2) than with B (Phase 2 only); however, we would also expect reciprocal overshadowing between B and Y during Phase 2 training to lessen spatial control by B alone relative to A, which received trials of A alone during Phase 1. Additional control

groups would be needed to determine which factor was responsible for the difference between A and B.

One concern with Experiment 1b could be that subjects did not detect the presence of X during Phase 2 in the ARENA preparation. With a distance of 34 cm between the target and LM X in ARENA, perhaps the pigeons failed to detect that X was present, thereby producing a blocking-like effect due to a complete failure of acquisition. Figure 4a displays the mean distributions of searches across the target location and the two response units to the left and right of the target on trials of A during the last trial of the last session of Phase 1 and the first trial of AX during the first session of Phase 2. The number of responses at each unit was standardized across trials, such that responses were recorded relative to the expected target on each trial. From the last trial of A during Phase 1 to the first trial of AX, we would expect the most change at the response unit to the right of X, where the subjects might search as a result of generalization from A. Figure 4a and 4b reveal several changes, including more responses at the generalization target location (1) during AX trials in Fig. 4a. By the last trial of AX, responding at the generalization target had decreased. These changes suggest that (1) subjects detected the new landmark and (2) subjects explored the environment enough to detect any new landmarks or targets. Consequently, the opportunity to learn about the value of X was present during training.

General discussion

Pigeons were trained to peck at a target location signaled by two landmarks (A+ and Z+) in a touchscreen-equipped chamber (Exp. 1a) or within an automated open field (ARENA, Exp. 1b). In the second phase, an additional landmark (X) was

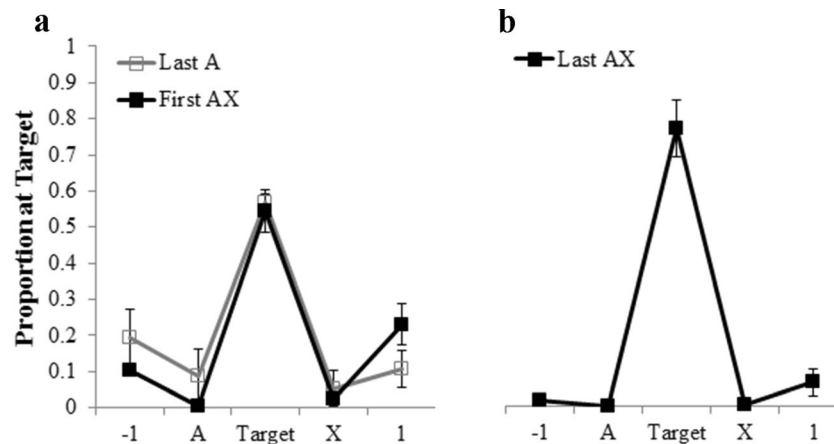


Fig. 4 **a** Mean distribution of searches across the target location and the two response units to the left and right of the target on each trial of Experiment 1b. The number of responses at each unit was standardized across trials, such that responses were recorded relative to the expected target on each trial. The response units occupied by landmarks during each trial are indicated on the *x*-axis; the units to the left and right of the landmarks on each trial are labeled as -1 (to left of the target and

landmark) and 1 (to the right of the target and landmark), respectively. The data are from the last A+ trial of Phase 1 and the first AX+ trial of Phase 2 in ARENA during Experiment 1b. **b** Mean distribution of searches across the target locations and the two response units to the left and right of the target during the last AX+ trial of Phase 2 in ARENA during Experiment 1b

presented in compound with trials of A (AX+) and the target. On separate trials, pecks to a target were reinforced in the presence of a second pair of novel landmarks (BY+) positioned in the same relationship to the target as AX. Test trials of each landmark alone were presented. Critically, spatial control by X was poor relative to control by A and Y. The results of Experiments 1a and 1b revealed no differences in the magnitudes or patterns of spatial control between the touchscreen and ARENA search tasks. These results provide the first evidence for a blocking effect with pigeons in the spatial domain.

After training with BY and the target during Phase 2 of Experiments 1a and 1b, test trials of B and Y alone revealed larger proportions of responses at the predicted target from training than at the generalization target. This was crucial, because more responding at the target location in the presence of each landmark required learning to respond in different directions from landmarks B and Y. This result indicates that subjects learned the B–target and Y–target spatial relationships and were not simply generalizing from other landmarks encountered during training (e.g., LMs A and Z). We also found evidence for learning of the X–target spatial relationship in Experiments 1a and 1b, but the key finding was that less spatial control was observed in the presence of X than of Y, which was not trained in the presence of an already established landmark.

The results from these experiments converge with a growing body of evidence suggesting that cue competition effects in the spatial domain are a subset of a more general associative-learning mechanism. Rodrigo et al. (1997) trained rats in a Morris pool to locate and swim to a hidden platform, and landmarks hanging over the perimeter of the pool were provided as extra-maze cues. Rodrigo et al. first verified that rats placed on the hidden platform in full view of four

landmarks for several trials were subsequently able to locate the hidden platform in the presence of only three landmarks. Rats in the blocking group were placed on the platform with landmarks A, B, and C suspended above the edge of the pool, whereas rats in the control group received identical trials but with a different set of landmarks (i.e., A', B', and C'). All groups then received four days of placement trials with the configuration of landmarks A, B, C, and X. At test, rats were placed in the pool to find the hidden target with only a subset of landmarks (e.g., A, B, and X), and performance showed a significant deficit in the blocking group relative to the control group. All groups were equally capable of predicting the quadrant of the hidden platform on the basis of LMs A, B, and C or A, B, C, and X, but the blocking group was deficient in preferring the quadrant of the platform signaled by the subset of LMs A, B, and X (but see Rodriguez, Chamizo, & Mackintosh, 2013, for the effects of sex differences). Similarly, humans trained to navigate a computerized version of a virtual pool with one set of landmarks performed poorly when tested on a second set of added landmarks (Hamilton & Sutherland, 1999), and honeybees trained to find reward in the presence of one cue failed to show spatial control by a subsequently added cue (Cheng & Spetch, 2001).

More recently, Stahlman and Blaisdell (2009) were able to capture spatial blocking among landmarks in an open-field foraging task in rats. The open field featured a 4 × 4 array of response cups, with food being buried under a single target cup. Adjacent landmarks could be placed to the left or right of the target cup. In Phase 1, rats were presented with A+ trials, during which LM A signaled the location of hidden food. In Phase 2, rats were given AX+ trials, in which X served as a redundant spatial cue to the location of food. Additionally, BY+ trials were given as a within-subjects overshadowing-

control procedure. At test, the rats received nonreinforced presentations of X and Y on separate trials. Rats took longer to find the training target location in the presence of X than of Y, thereby demonstrating that spatial control by X was blocked by prior learning with A. Obtaining spatial blocking in an avian model has not been reported with an open field or touchscreen apparatus.

The blocking effect is a hallmark of an associative process. Early attempts to characterize spatial learning suggested that it was specialized and modular, sharing little with other types of learning (Cheng 1986; O'Keefe & Nadel, 1978). More recent characterizations have identified two systems of spatial learning: landmark learning, which is immune to associative effects (i.e., locale system), and beacon homing, which is not (e.g., taxon system; O'Keefe & Nadel, 1978). Much evidence has been required in order to encourage thinking about landmark learning as another instance of associative learning. In the present experiments, we found a deficit in spatial accuracy in the presence of a blocked landmark closely resembling the deficit in the magnitude of responding reported in more conventional classical and operant-conditioning tasks. These results add pigeons to the list of species demonstrating spatial blocking, which also includes humans (e.g., Hamilton & Sutherland, 1999), rats (e.g., Biegler & Morris, 1999; Chamizo, Sterio, & Mackintosh, 1985; Rodrigo et al., 1997; Stahlman & Blaisdell, 2009), and honeybees (e.g., Cheng & Spetch, 2001).

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